Plant traits inform predictions of tundra responses to global change

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Plant traits inform predictions of tundra responses to global change

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Summary

In the rapidly warming tundra biome, plant traits provide an essential link between ongoing vegetation change and feedbacks to key ecosystem functions. However, only recently have comprehensive trait data been compiled for tundra species and sites, allowing us to assess key elements of functional responses to global change. In this review, we summarize trait-based research in tundra ecosystems, with a focus on three components: plant trait variation and how it compares with global patterns; shifts in community-level traits in response to environmental change; and the use of traits to understand and predict ecosystem function. Quantifying patterns and trends in plant traits will allow us to better project the consequences of environmental change for the ecology and functioning of tundra ecosystems.

Keywords: climate, decomposition, ecosystem function, environmental filtering, plant functional trait, trait variation, tundra, vegetation change

I. Introduction

Traits, the measurable properties of living organisms describing structure and function, can be used to understand and quantify community change (Reich, 2014). Trait-based ecology asserts that the properties and functioning of any ecosystem can be related to the phenotypic traits of its resident species (McGill *et al.*, 2006). This 'traits manifesto' (Reich, 2014) has seen a dramatic rise in popularity in recent years improving our understanding of community assembly (Siefert *et al.*, 2015) and ecosystem responses to warming (Soudzilovskaia *et al.*, 2013). However, progress is hampered by fundamental unknowns regarding the nature of trait variation and physiological trade-offs (Siefert *et al.*, 2015; Díaz *et al.*, 2016; Shipley *et al.*, 2016), by issues of prediction across scales (Messier *et al.*, 2017), and by uneven data coverage among traits, species, and ecosystems (Iversen *et al.*, 2015; Jetz *et al.*, 2016; Bjorkman *et al.*, 2018). For trait-based ecology to reach its full potential, trait-function relationships must be tested across the world's biomes, including in our planet's most extreme environments.

The Arctic is warming at twice the global average rate (IPCC, 2014) and alpine ecosystems are experiencing dramatic changes in snow regimes and glacial melt (Ernakovich *et al.*, 2014). Warming has been linked to widespread tundra vegetation change, including an increase in shrub and graminoid abundance and a decline in bare ground (Myers-Smith *et*

al., 2011; Elmendorf *et al.*, 2012b; Pearson *et al.*, 2013). The traits of tundra plants, including maximum height, specific leaf area (SLA) and leaf dry matter content (LDMC), may also be responding to the changing growing conditions (Sundqvist *et al.*, 2011; Hudson *et al.*, 2011; Baruah *et al.*, 2017; Bjorkman *et al.*, 2018). Such vegetation and trait changes can alter ecosystem functions such as nutrient cycling, decomposition rates, and albedo, with potential feedbacks to soil carbon storage and the global carbon cycle (Sturm, 2005; Cornelissen *et al.*, 2007).

Trait-based approaches could allow for better quantification of the impacts of global change on ecosystem functions and resulting climate feedbacks. Tundra trait-based ecology is especially critical as tundra ecosystems represent some of the most rapidly changing places on the planet. However, until recently, the temperature-limited plant communities found above treeline in Arctic and alpine tundra regions have been underrepresented in global trait-based databases and analyses (Kattge *et al.*, 2011; Bjorkman *et al.*, 2018). Despite rapid ecological change, the tundra has featured in less than 3% of plant trait research in the last decade (August 2018 web of science search for ‘plant functional trait’ OR ‘plant trait’ and ‘plant functional trait’ OR ‘plant trait’ AND 'tundra' OR ‘Arctic’ OR ‘Alpine’ from 2008 to 2018 in the fields of ‘ecology’ or ‘plant sciences’) and comprises less than 5% of data in TRY, the largest available database of plant traits (Moles *et al.*, 2009; Kattge *et al.*, 2011; Bjorkman *et al.*, 2018). However, recent data collection is beginning to fill this ‘trait data gap’ (Figure 1; (Bjorkman *et al.*, 2018), enabling large-scale trait-based syntheses that provide new insights into ecological change and the resultant feedbacks to ecosystem process in the northern and high elevation regions of the planet (Prevéy *et al.*, 2017; Steinbauer *et al.*, 2018; Bjorkman *et al.*, 2018).

II. The global context of tundra trait variation

The tundra provides an ideal ‘natural laboratory’ in which to test many fundamental questions of trait-based ecology. It is in the tundra biome, where many plant communities have relatively low species richness (Jetz *et al.*, 2016; Bjorkman *et al.*, 2018) , that near-total trait coverage can be achieved in community-level analyses. By capturing traits for all component species in tundra plant communities, fundamental questions about the roles of immigrant, locally extinct, common and rare species to changes in ecosystem functions can be estimated in a way that is not possible in other of the world’s ecosystems. Extreme environmental conditions and large species ranges allow for tests of our current understanding of environmental filtering (Shipley *et al.*, 2016), trait-trait relationships (Díaz *et al.*, 2016), and sources of trait variation (Siefert *et al.*, 2015). Tundra trait distributions are thought to be largely determined by climatic conditions and are associated with small plant

size and conservative economic strategies (Molau, 1993). However, short growing seasons also drive high relative growth rates (Chapin, 1987) and leaf nitrogen concentrations (Körner, 1989). Consequently, it is unclear whether environment filters tundra trait distributions to the same extent as in other biomes within multivariate trait space, particularly for traits associated with resource economics (Figure 2). Tundra plants may thus exhibit unique trait relationships resulting from adaptation to extreme environmental conditions.

Functional groups alone do not capture tundra trait variation

Large geographical ranges of tundra species and convergence in trait expression in the tundra could also challenge the assumption that the majority of trait variation occurs among species or functional groups (Díaz *et al.*, 2016; Shipley *et al.*, 2016); Figure 2). Much of our existing understanding of vegetation change in the tundra biome has been assessed at the functional group level (Henry & Molau, 1997; Elmendorf *et al.*, 2012a,b). However, traditional tundra functional groups (e.g., deciduous and evergreen shrubs, graminoids and forbs) do not explain the majority of trait variation in the most commonly measured traits (Thomas *et al.*, in press). Intraspecific trait variation has also been demonstrated to mediate community assembly (Kichenin *et al.*, 2013) and warming responses in the tundra (Baruah *et al.*, 2017). Furthermore, genetic differentiation and local adaptation in leaf and phenological traits is evident in several widespread tundra species (Bjorkman *et al.*, 2017). High within-species variation may reduce the ability of species or functional group approaches to improve our understanding of plant community responses to environmental change (Saccone *et al.*, 2017; Anderegg *et al.*, 2018).

III. The current state of knowledge on trait change in the tundra biome

Predicting the consequences of climate change for tundra plant traits requires a mechanistic understanding of the drivers of trait variation across scales. Much of what we know about the causes of trait variation globally relies on correlational relationships between traits and environmental variables (e.g., temperature) over space (Moles *et al.*, 2009; Asner *et al.*, 2016). Space-for-time substitution can thus inform projections of trait shifts over time as the environment changes. In the tundra, many community-level traits, including maximum height, specific leaf area (SLA) and leaf dry matter content (LDMC), vary significantly with temperature over large spatial scales (Figure 3). However, water availability frequently influences the strength (SLA, LDMC) and even the direction (leaf nitrogen, leaf area) of these temperature-trait relationships (Bjorkman *et al.*, 2018).

Strong temperature-trait relationships do not predict change over time for all tundra traits

Strong temperature-trait relationships across space suggest that climate warming may alter traits (Figure 3). However, spatial gradients do not necessarily align with change over time, particularly where barriers to migration or other time lags may limit community response to change (Elmendorf *et al.*, 2015). Increases in community or individual plant height have been widely documented at individual tundra sites (Hudson *et al.*, 2011; Myers-Smith *et al.*, 2011; Baruah *et al.*, 2017), linked to experimental warming (Hudson *et al.*, 2011; Elmendorf *et al.*, 2012a), higher summer temperatures (Elmendorf *et al.*, 2012b), increasing nutrient availability (Zamin & Grogan, 2012), and altered snow depth (Wahren *et al.*, 2005). Warming and earlier snowmelt are also associated with larger leaves, greater reproductive effort, and in some cases with earlier plant phenology (Arft *et al.*, 1999). However, a synthesis of trait change across more than 100 tundra sites indicates that only community canopy height has changed consistently over the past three decades (Bjorkman *et al.*, 2018). This increase in height was primarily due to the immigration of taller species into existing communities from either the local species pool or more distant plant communities, and was correlated with changes in temperature over the same period.

IV. The links between traits and ecosystem functions

A major challenge for plant ecologists is understanding how observed and predicted vegetation changes are likely to influence ecosystem functioning. In tundra ecosystems, mechanistic links between functional traits and ecosystem function offer opportunities to understand the impacts of vegetation change and to quantify climate change feedbacks (Figure 4). Albedo (surface reflectance) and energy balance are associated with morphological traits, including canopy height and leaf area (Sturm, 2005; Blok *et al.*, 2010). For example, the lower albedo of shrub canopies may enhance warming (Sturm, 2005), particularly in spring when stems protrude from the snowpack (Bonfils *et al.*, 2012). Taller and denser canopies trap snow in winter, increasing soil temperatures by 3-10˚C (Chapin *et al.*, 2005), but also increase shade in summer, protecting permafrost soils (Blok *et al.*, 2010). Phenological and reproductive traits determine trophic interactions and thus have potentially far-reaching impacts within tundra ecosystems (Cleland *et al.*, 2012; Oberbauer *et al.*, 2013; Prevéy *et al.*, 2017).

Trait change could feedback to either increase or decrease tundra carbon storage

Trait change could form an important feedback to global biogeochemical cycling through alterations to the high latitude carbon pool, which comprises 28 – 38% of global soil (Hugelius *et al.*, 2013). Leaf traits exert strong controls over litter decomposition in the tundra, outweighing among-site differences (Sundqvist *et al.*, 2011), experimental warming

(Hobbie, 1996), and snow depth (Baptist *et al.*, 2010). Litter quality also affects decomposition of older carbon by stimulating microbial communities (Kuzyakov *et al.*, 2000), and determines rates of biogeochemical cycling (Reich, 2014). Trait change may thus decrease (Cornelissen *et al.*, 2007) or increase litter decomposition, nutrient cycling and carbon storage (Hobbie, 2015), though the size and direction of this effect remains unknown. Below ground traits such as rooting depth (Iversen *et al.*, 2015) and the phenology of root growth (Blume-Werry *et al.*, 2016) could shift under warming climates with thawing permafrost soils, thus altering above-below ground plant allocation and carbon storage.

Above-below ground tundra biomass allocation could differ due to freeze-thaw dynamics
Finally, ecosystem carbon balance depends on trade-offs between decomposition and carbon uptake in biomass (Sistla *et al.*, 2013). Carbon storage in plant biomass will likely increase (Weintraub & Schimel, 2005) as a result of relationships between temperature and traits associated with high productivity (Elmendorf *et al.*, 2015; Steinbauer *et al.*, 2018; Bjorkman *et al.*, 2018), longer growing seasons (Oberbauer *et al.*, 2013), increased plant size (Hudson *et al.*, 2011) and woodiness (Hobbie, 1996; Myers-Smith *et al.*, 2011; Pearson *et al.*, 2013). However, increased carbon uptake above ground may be offset by below-ground losses (Sistla *et al.*, 2013; though see Lafleur & Humphreys, 2018). Quantifying tundra ecosystem carbon balance thus requires an improved understanding of below-ground traits such as root biomass and mycorrhizal association, which remain particularly challenging to measure in permafrost soils (Iversen *et al.*, 2015).

V. Future priorities for tundra trait research

Most evidence for changes in tundra plant traits thus far comes a small number of particularly well-monitored locations (Figure 1). Substantial variation in vegetation change at landscape and regional scales (Elmendorf *et al.*, 2012a,b; Guay *et al.*, 2014; Bjorkman *et al.*, 2018) suggests that data collection beyond the most intensively monitored sites is a future research priority. Furthermore, current studies of plant trait change focus entirely on above-ground traits. With up to 90% of tundra biomass located below ground, we require new data collection to quantify how below-ground traits are changing across the tundra biome (Iversen *et al.*, 2015). Thus, future research priorities include quantifying the diversity of trait responses above and below ground, across the landscape and across trophic levels, and linking this change directly to key ecosystem functions (Bardgett *et al.*, 2013; Gauthier *et al.*, 2013).

Conclusions

Recent evidence indicates that ecological change in the tundra can be confidently attributed to climate warming (Elmendorf *et al.*, 2012b; IPCC, 2014; Elmendorf *et al.*, 2015; Myers-Smith *et al.*, 2015; Prevéy *et al.*, 2017), yet the mechanisms and trajectories of community and trait change are complex (Bjorkman *et al.*, 2018). Trait-based ecology can inform our understanding of tundra functional change in ways that vegetation monitoring of species composition and coarse-resolution remote sensing of above-ground biomass alone cannot (Jetz *et al.*, 2016). Tundra plant trait analyses indicate that traits such as plant height are increasing rapidly (Elmendorf *et al.*, 2012b; Bjorkman *et al.*, 2018), yet others such as leaf traits have not undergone change at the community-level despite varying strongly across biogeographic gradients (Bjorkman *et al.*, 2018).

The substantially different rates of change among traits can inform our predictions of which functional changes will be particularly rapid with future warming. Functions associated with plant height, such as albedo, are likely to change more rapidly than feedbacks involving changes in litter decomposability and soil nutrient processing due to the rates of change observed for these different community-level traits (Bjorkman *et al.*, 2018). However, most trait-based research has so far focused on the above-ground component of tundra ecosystems, limiting our understanding of below-ground trait responses to global change (Iversen *et al.*, 2015). Incorporating current and future tundra trait research into Earth system models (Wullschleger *et al.*, 2014; Fisher Rosie A. *et al.*, 2017; Butler *et al.*, 2017), will allow plant functional traits to fulfil their promise of improving our understanding of community responses and feedbacks to ongoing global change, a particularly urgent need in the rapidly warming tundra biome.

References

Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J. **2018**. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* **21**: 734–744.

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, *et al.* 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* **69**: 491–511.

Asner GP, Knapp DE, Anderson CB, Martin RE, Vaughn N. **2016**. Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences* **113**: E4043–E4051.

Baptist F, Yoccoz NG, Choler P. **2010**. Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant and Soil* **328**: 397–410.

Bardgett RD, Manning P, Morriën E, Vries FTD. **2013**. Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle. *Journal of Ecology* **101**: 334–343.

Baruah G, Molau U, Bai Y, Alatalo JM. **2017**. Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. *Scientific Reports* **7**: 2571.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PSA, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC, *et al.* 2018. Plant functional trait change across a warming tundra biome. *Nature* **562**: 57–62.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Thomas HJD, Alatalo JM, Alexander H, Anadon-Rosell A, Angers-Blondin S, Bai Y, *et al.* 2018. Tundra Trait Team: A database of plant traits spanning the tundra biome. *Global Ecology and Biogeography*. http://dx.doi.org/10.1111/geb.12821

Bjorkman AD, Vellend M, Frei ER, Henry GHR. **2017**. Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic. *Global Change Biology* **23**: 1540–1551.

Blok D, Heijmans MMPD, Schaepman-Strub G, Kononov A V., Maximov TC, Berendse F. **2010**. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology* **16**: 1296–1305.

Blume-Werry G, Wilson SD, Kreyling J, Milbau A. **2016**. The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytologist* **209**: 978–986.

Bonfils CJW, Phillips TJ, Lawrence DM, Cameron-Smith P, Riley WJ, Subin ZM. **2012**. On the influence of shrub height and expansion on northern high latitude climate. *Environmental Research Letters* **7**: 015503.

Butler EE, Datta A, Flores-Moreno H, Chen M, Wythers KR, Fazayeli F, Banerjee A, Atkin OK, Kattge J, Amiaud B, *et al.* 2017. Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences*: 201708984.

Chapin FS. **1987**. Environmental Controls over Growth of Tundra Plants. *Ecological Bulletins* **38**: 69–76.

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, *et al.* 2005. Role of land-surface changes in arctic summer warming. *Science* **310**: 657–60.

Cleland EE, Allen JM, Crimmins TM, Dunne JA, Pau S, Travers SE, Zavaleta ES, Wolkovich EM. **2012**. Phenological tracking enables positive species responses to climate change. *Ecology* **93**: 1765–1771.

Cornelissen JHC, van Bodegom PM, Aerts R, Callaghan T V, van Logtestijn RSP, Alatalo J, Chapin FS, Gerdol R, Gudmundsson J, Gwynn-Jones D, *et al.* 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* **10**: 619–27.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice CI, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan T V, Collier LS, Cooper EJ, Cornelissen JHC, Day TA, *et al.* 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* **15**: 164–175.

Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG, *et al.* 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* **2**: 453–457.

Elmendorf SC, Henry GHR, Hollister RD, Fosaa AM, Gould WA, Hermanutz L, Hofgaard A, Jónsdóttir II, Jorgenson JC, Lévesque E, *et al.* 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences* **112**: 448–452.

Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD. **2014**. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*.

Fisher Rosie A., Koven Charles D., Anderegg William R. L., Christoffersen Bradley O., Dietze Michael C., Farrior Caroline E., Holm Jennifer A., Hurtt George C., Knox Ryan G., Lawrence Peter J., *et al.* 2017. Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology* **24**: 35–54.

Gauthier G, Bêty J, Cadieux M-C, Legagneux P, Doiron M, Chevallier C, Lai S, Tarroux A, Berteaux D. **2013**. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**: 20120482.

Guay KC, Beck PS a, Berner LT, Goetz SJ, Baccini A, Buermann W. **2014**. Vegetation productivity patterns at high northern latitudes: A multi-sensor satellite data assessment. *Global Change Biology*: 3147–3158.

Henry GHR, Molau U. **1997**. Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology* **3**: 1–9.

Hobbie SE. **1996**. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**: 503–522.

Hobbie SE. **2015**. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in Ecology and Evolution* **30**: 357–363.

Hudson JMG, Henry GHR, Cornwell WK. **2011**. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology* **17**: 1013–1021.

Hugelius G, Tarnocai C, Broll G, Canadell JG, Kuhry P, Swanson DK. **2013**. The Northern Circumpolar Soil Carbon Database: spatially distributed datasets of soil coverage and soil carbon storage in the northern permafrost regions. *Earth System Science Data* **5**: 3–13.

IPCC. **2014**. Climate change 2014: impacts, adaptation, and vulnerability. *Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*: 1042.

Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschleger SD. **2015**. The unseen iceberg: plant roots in arctic tundra. *New Phytologist* **205**: 34–58.

Jetz W, Cavender-Bares J, Pavlick R, Schimel D, Davis FW, Asner GP, Guralnick R, Kattge J, Latimer AM, Moorcroft P, *et al.* 2016. Monitoring plant functional diversity from space. *Nature Plants* **2**: 1–5.

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, *et al.* 2011. TRY - a global database of plant traits. *Global Change Biology* **17**: 2905–2935.

Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT. **2013**. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology* **27**: 1254–1261.

Körner C. **1989**. The nutritional status of plants from high altitudes. *Oecologia* **81**: 379–391.

Kuzyakov Y, Friedel JK, Stahr K. **2000**. Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry* **32**: 1485–1498.

Lafleur P, Humphreys E. **2018**. Tundra shrub effects on growing season energy and carbon dioxide exchange. *Environmental Research Letters* **13**: 055001.

McGill BJ, Enquist BJ, Weiher E, Westoby M. **2006**. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**: 178–185.

Messier J, McGill BJ, Enquist BJ, Lechowicz MJ. **2017**. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography* **40**: 685–697.

Molau U. **1993**. Relationships between Flowering Phenology and Life History Strategies in Tundra Plants. *Arctic and Alpine Research* **25**: 391.

Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, Pitman A, Hemmings FA, Leishman MR. **2009**. Global patterns in plant height. *J Ecol* **97**: 923–932.

Myers-Smith IH, Elmendorf SC, Beck PS, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback S, Macias-Fauria M, Forbes BC, *et al.* 2015. Climate sensitivity of shrub growth across the tundra biome. *Nature Clim. Change*: 887–891.

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, *et al.* 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* **6**: 045509.

Oberbauer SF, Elmendorf SC, Troxler TG, Hollister RD, Rocha A V, Bret-Harte MS, Dawes MA, Fosaa AM, Henry GHR, Høye TT, *et al.* 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **368**: 20120481.

Pearson RG, Phillips SJ, Loranty MM, Beck PS a., Damoulas T, Knight SJ, Goetz SJ. **2013**. Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change* **3**: 673–677.

Prevéy J, Vellend M, Rüger N, Hollister RD, Bjorkman AD, Myers-Smith IH, Elmendorf SC, Clark K, Cooper EJ, Elberling B, *et al.* 2017. Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Global Change Biology* **23**: 2660–2671.

Reich PB. **2014**. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology* **102**: 275–301.

Saccone P, Hoikka K, Virtanen R. **2017**. What if plant functional types conceal species-specific responses to environment? Study on arctic shrub communities. *Ecology* **98**: 1600–1612.

Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. **2016**. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*: 1–9.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso M V., *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406–1419.

Sistla SA, Moore JC, Simpson RT, Gough L, Shaver GR, Schimel JP. **2013**. Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature* **497**: 615–8.

Soudzilovskaia NA, Elumeeva TG, Onipchenko VG, Shidakov II, Salpagarova FS, Khubiev AB, Tekeev DK, Cornelissen JHC. **2013**. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences* **110**: 18180–18184.

Steinbauer MJ, Grytnes JA, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E, *et al.* 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* **556**: 231–234.

Sturm M. **2005**. Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research* **110**: G01004.

Sundqvist MK, Giesler R, Wardle DA. **2011**. Within- and across-species responses of plant traits and litter decomposition to elevation across contrasting vegetation types in subarctic tundra. *PLoS ONE* **6**: e27056.

Thomas HJD, Myers-Smith IH, Bjorkman AD, Elmendorf SC, Blok D, Cornelissen JHC, Forbes BC, Hollister RD, Normand S, Prevéy JS, *et al.* in press. Traditional plant functional groups poorly explain plant trait variation in the tundra biome. *Global Ecology and Biogeography (ref: GEB-2017-0415)*.

Wahren C-HA, Walker MD, Bret-Harte MS. **2005**. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* **11**: 537–552.

Weintraub MN, Schimel JP. **2005**. Nitrogen Cycling and the Spread of Shrubs Control Changes in the Carbon Balance of Arctic Tundra Ecosystems. *BioScience* **55**: 408.

Wullschleger SD, Epstein HE, Box EO, Euskirchen ES, Goswami S, Iversen CM, Kattge J, Norby RJ, Van Bodegom PM, Xu X. **2014**. Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany* **114**: 1–16.

Zamin TJ, Grogan P. **2012**. Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. *Environmental Research Letters* **7**: 034027.

Fig. 1 Map of currently available georeferenced trait data for tundra ecosystems above 40°N. Observations represent a combination of data from the TRY database (https://www.try-db.org/; 22066 observations) and newly available data from the Tundra Trait Team database (https://tundratraitteam.github.io/; 82203 observations). TRY trait data were filtered to include only likely tundra (Arctic or alpine) habitats. We first extracted all points above 65°N (Arctic tundra), then those points between 60 and 65°N that occurred above 1000 m in elevation, then those points between 55 and 60 °N that occurred above 1500 m in elevation, and finally points south of 55 °N that occurred above 2500 m in elevation. Circle colours represent the kind of trait (leaf, structural, chemical, rooting depth and root : shoot

ratios) while the size of the circle represents the relative number of observations in that location.

Fig. 2 Hypothesized location of tundra trait space within global trait space, and possible sources of trait variation. Global trait space is conceptualized as a 'galactic plane' defined by two major axes of trait variation, corresponding to strategies of plant size and resource economics (Díaz *et al.*, 2016). Tundra trait space could be constrained along both size and economic dimensions (1), along only the size dimension (2), or exhibit no strong constraints (3). Trait variation could be primarily expressed among species (a), or could exhibit high within-species variation, with larger overlap between species-level or functional group-level traits (b).

Fig. 3 Responses of six key plant traits to temperature across five different study types including: (1) temperature–trait relationship (community-level analyses based on a community-weighted trait means (CWM) at sites across a temperature gradient); (2) temperature–trait relationship (intraspecific analysis based on multiple populations of the same species across a temperature gradient); (3) *in situ* warming experiments; (4) temperature sensitivity (correspondence between interannual variation in traits and temperature); and (5) change over time (temporal trends). Green arrows, temperature–trait relationships in wet sites; orange arrows, temperature–trait relationship in dry sites; pink arrows, temperature–trait relationships with summer temperatures, blue arrows, temperature–trait relationships with winter temperatures; purple arrows, temperature–trait relationships to both winter and summer temperatures; grey arrows, temporal analyses. Solid arrows indicate relationships based on cross-site synthesis, dashed arrows indicate the findings of individual site or species-specific studies.

Fig. 4 Trait change links to ecosystem functions such as surface albedo, energy balance, soil temperature, biogeochemical cycling and carbon storage. Changes in these key ecosystem functions could create feedbacks to the global climate system. Currently the direction and magnitudes of many of these feedbacks remain uncertain. Trait data and analyses have the potential to fill in the gaps in ecological data syntheses and Earth System models to improve the quantification of the ecological feedbacks of tundra ecosystem change (Wullschleger *et al.*, 2014).

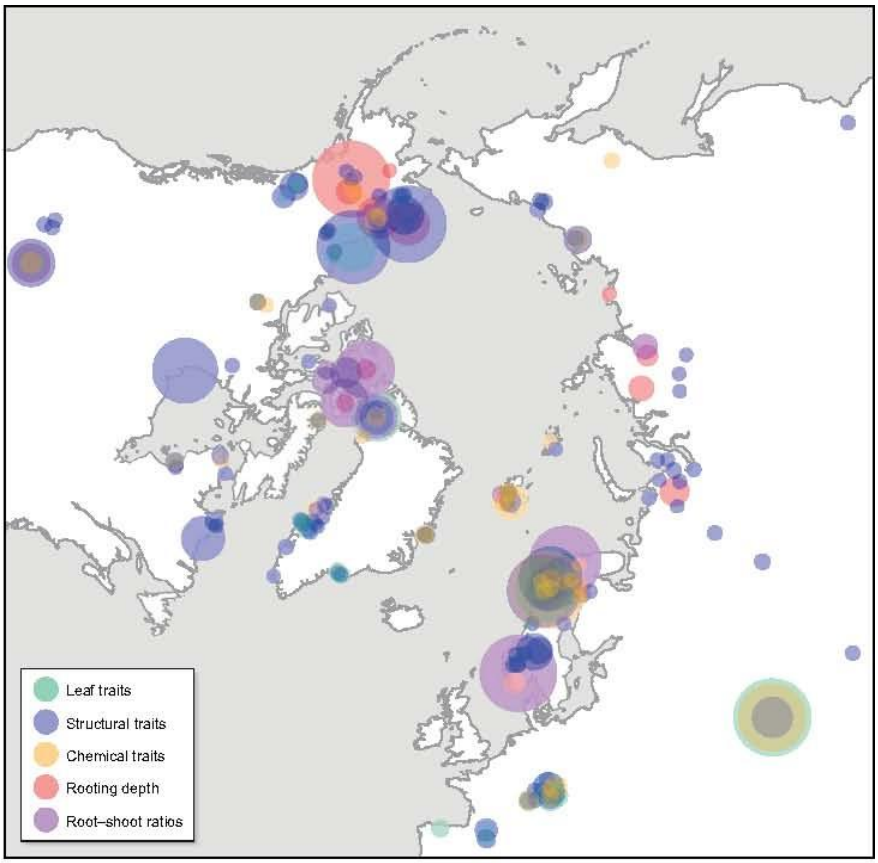

Figure 1

Tansley Insight 27206

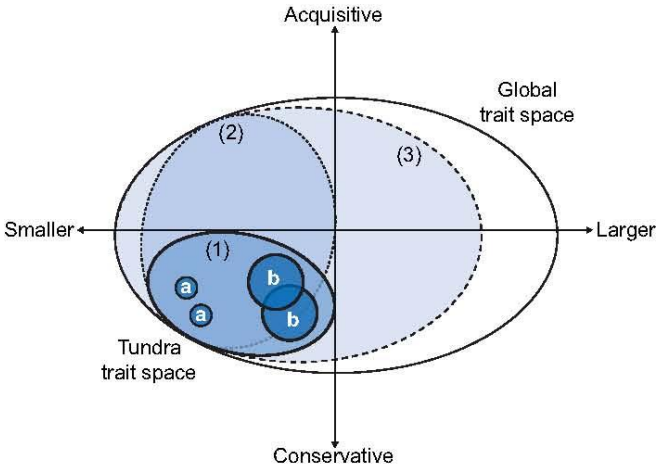

Figure 2

Tansley Insight 27206

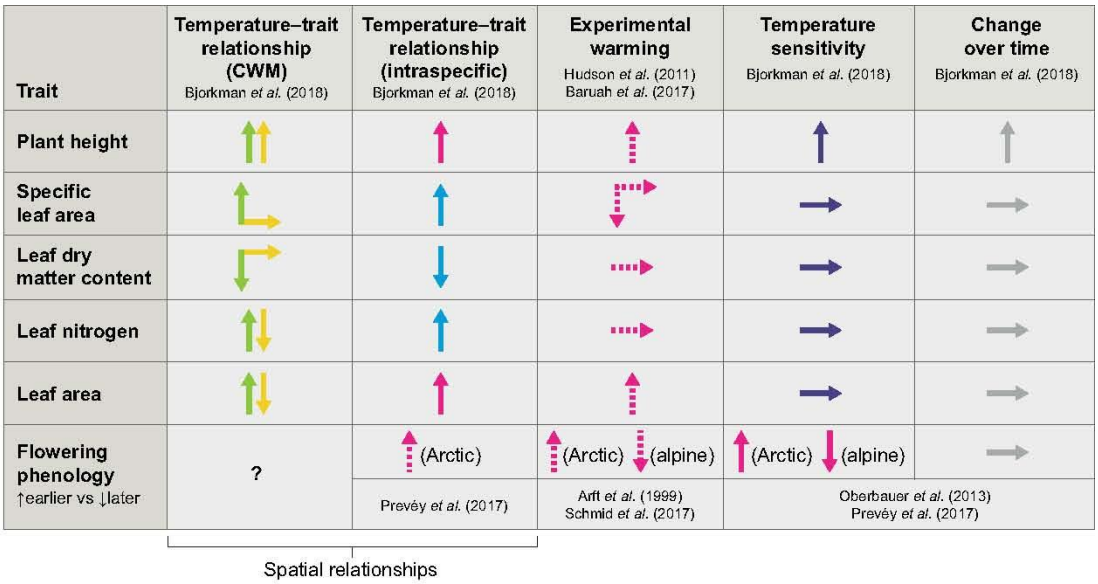

Figure 3

Tansley Insight 27206

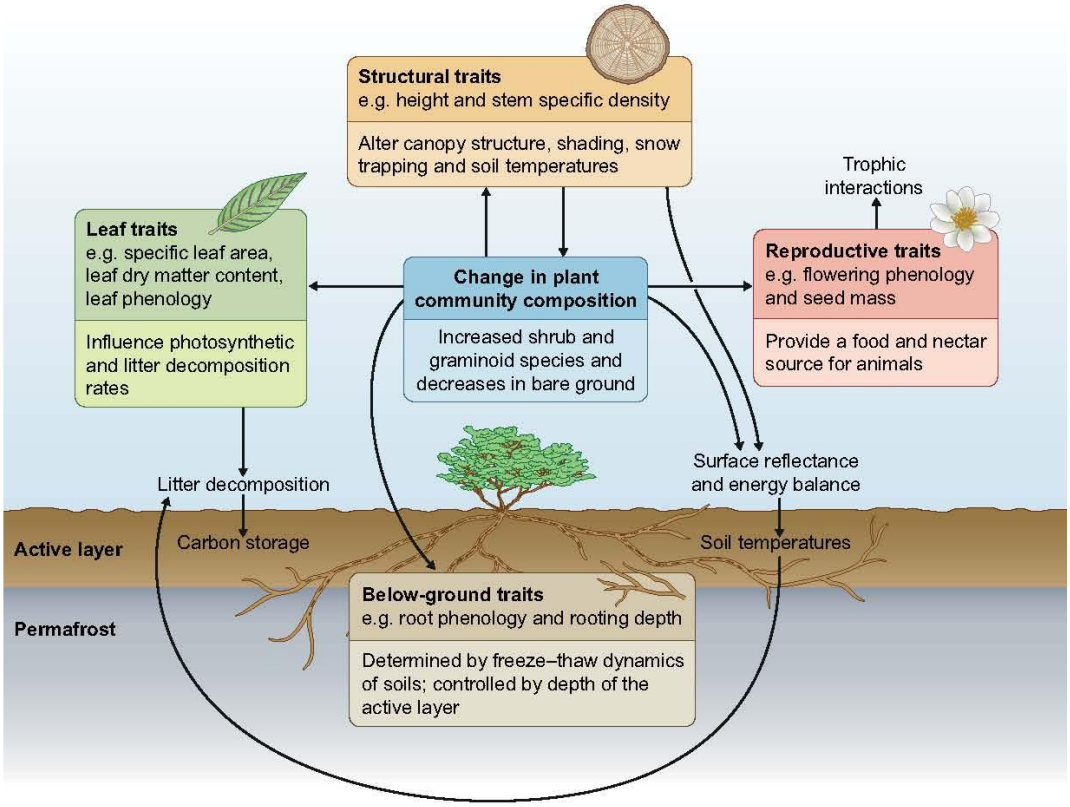

Figure 4

Tansley Insight 27206